Connecting Earth Observation to High-Throughput Biodiversity Data

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Preface

There is much interest in using Earth Observation (EO) technology to track biodiversity, ecosystem functions, and ecosystem services, understandable given the fast pace of biodiversity loss. However, because most biodiversity is invisible to EO, EO-based indicators could be misleading, which can reduce the effectiveness of nature conservation and even unintentionally decrease conservation effort. We describe an approach that combines automated recording devices, high-throughput DNA sequencing, and modern ecological modelling to extract much more of the information

available in EO data. This approach is achievable now, offering efficient and near-real-time monitoring of management impacts on biodiversity and its functions and services.

Meeting the Aichi Biodiversity Targets

From Google Earth to airborne sensors, the Copernicus Sentinels, and cube satellites, Earth Observation is undergoing a rapid expansion in capacity, accessibility, resolution, and signal-to-noise ratio, resulting in a recognised shift in our capability for using remote-sensing technologies to monitor biophysical processes on land and water[1-3]. These advances are motivating calls to use Earth Observation products to manage our natural environment and to track progress toward global and national policy targets on biodiversity and ecosystem services[4-6]. Foremost among these policies are the Strategic Plan for Biodiversity and the Aichi Biodiversity Targets, which were adopted in 2010 by the Parties to the Convention on Biological Diversity (CBD) to "take effective and urgent action to halt the loss of biodiversity in order to ensure that by 2020 ecosystems are resilient and continue to provide essential services…"[7]. The United Nations Sustainable Development Goals[8] now include some of the Aichi Targets, and the 2015 Paris Agreement has reiterated the commitments of the UN Framework Convention on Climate Change to reducing emissions from deforestation and forest degradation

(REDD+) and to securing non-carbon benefits, which include biodiversity and ecosystem services[9].

However, we have struggled to track and report progress toward the Aichi Targets in a standardised and comprehensive way[10]. Although almost two-thirds of the CBD Parties have updated their National Biodiversity Strategies and Action Plans to reflect the 2010 revisions, many still do not contain measurable indicators on the state of biodiversity, let alone ecosystem services. This lack of quantification conceals the impacts of policy and management interventions on biodiversity and ecosystem functions and services[11]. The difficulty of designing indicators[12-14] has prompted an international consortium of biodiversity scientists called GEO BON (Group on Earth Observations' Biodiversity Observation Network) to propose a framework of Essential Biodiversity Variables[15], with the aim of setting minimum standards of coverage to ensure informativeness and to harmonise disparate local measures so that biodiversity and ecosystem data can be compared over space and time. The Essential Biodiversity Variables thus measure the 'state of biodiversity' at multiple levels: genetic composition, species populations, species traits, community composition, ecosystem structure, and ecosystem function[15].

Although it was originally envisioned that most of the variables (genetic to community composition) would be scaled up from "intensive *in-situ* measurements"[15] taken on the

97 ground, such measurements are costly and difficult because they are traditionally
98 gathered by visual and aural detection of plants and animals in the wild (preceded by
99 months or years of observer practice) and by mass collection of organisms (followed by
100 months of identification from morphology), so that data collection is slowed by human-
101 caused bottlenecks in sampling and taxonomy[16].

102 As a result, attention is now being focused on designing 'Satellite Remote Sensing-
103 Essential Biodiversity Variables' (SRS-EBVs) to enable cost-effective and global-scale
104 monitoring[5,6,12]. The problem here is that only a few Earth Observation products can be
105 mapped directly to Essential Biodiversity Variables and then to Aichi Targets, because
106 these products primarily measure gross vegetation and landscape metrics, such as land
107 cover and phenology[4]. For example, Pettorelli et al.[12] found only two Earth Observation
108 products (net primary productivity and fire incidence) that could serve as Essential
109 Biodiversity Variables for the Sahara, despite this biome's suitability for remote sensing
110 due to its visible biodiversity hotspots, remoteness, and availability of long time series.
111 Many of the Aichi Targets require data with species-level resolution, either because some
112 species are direct policy targets (e.g. Target 9: "invasive species controlled or eradicated")
113 or because species compositional data define the metric (e.g. Target 11: "protected areas
114 are ecologically representative and conserved effectively").

Clearly, a radically new approach is required if progress towards the Aichi Targets is to be accelerated, one that is robust, widely affordable, and can record stocks and changes in biodiversity and ecosystem services consistently, continuously, and at high resolution over large geographic scales. Here, we present such an approach in a framework that exploits recent efficiency gains and analytical breakthroughs in sensors, computation, ecology, taxonomy, and genomics (**Figure 1, Box 1**).

Box 1. Inferring a Hidden Ecosystem Function from Space

Large-bodied Amazonian monkeys are responsible for a key ecosystem function: they are the primary dispersers of large seeds, which are associated with more carbon-dense tree species. Peres et al.[17] have proposed that this function boosts forest carbon storage. The idea can be tested by using Earth Observation data and public records to map human settlements and transport corridors and predict where monkey populations have declined through hunting[17,18]. We can then use on-the-ground sampling and airborne sensors to test whether forests that have had longer exposure to hunting lack monkey populations and have more low-carbon-density tree species dispersed by wind and birds. In short, by combining Earth-Observation-derived maps of human activity with empirical observations of the response of primate populations to that activity, it should be

possible to map and track an ecosystem function (large-seed dispersal) that is invisible to satellites but contributes to an important ecosystem service (climate regulation).

From Point Samples to Continuous Maps

Instead of trying to map Earth Observation (EO) products directly to biodiversity, as encapsulated by SRS-EBVs[4-6,12], we propose to extract more information from EO data by interpolating biodiversity point samples to build continuous landscape maps of species distributions (**Figure 1**)[19]. Because it is species that are mapped, it then becomes possible to layer on the vast biological knowledge that we have collectively built up over decades of research, including historical distributions, phylogenetic relationships, and knowledge of species traits and interactions to infer, map, and track the distributions of ecosystem functions and services (**Box 1**). This approach, which we call here **CEOBE** (Connecting Earth Observation to Biodiversity and Ecosystems), is possible because of (1) major advances in EO sensitivity and capacity, (2) more efficient techniques to collect biodiversity data on the ground, and (3) modern community-analysis models from statistical ecology. We now review each of these advances, with additional detail in Supplementary Information.

The New Era of Earth Observation

There are ten times as many satellites in operation now as there were in the 1970s, a result of increasing sensor longevity and a six-fold increase in launches[20]. Spatial resolution has improved to less than 1 m in both optical and radar sensors. Data continuity is also being maintained, most directly by the launch of NASA's Landsat 8 in 2013, which extends and technically enhances the 40-year Landsat record of medium-resolution, multispectral surface observations[21]. Data continuity is a key factor in understanding changes in biodiversity, as threats to biodiversity impact at a range of scales and often across lengthy timespans[22].

The long-term Landsat record is being enhanced by new satellite systems and multiple sensors in a global network, a 'virtual constellation' that may help overcome problems in terrestrial monitoring from single sensors[2]. As part of the Copernicus program, the ESA Sentinel satellites are the latest addition to the global network. With six missions planned and the first three launched, the Sentinels have radar, optical sensors, radiometers, and spectrometers with different goals[23]. Sentinel-1, the radar satellite, and Sentinel-2, the superspectral high-resolution mission, are of particular interest to biodiversity monitoring, with long-term continuity of measurements, global coverage, and quick revisit times [24,25].

170 There have also been developments in hyperspectral sensors with EnMAP, HyspIRI,
171 PRISMA, and FLEX imaging spectrometer missions planned[1]. In addition, airborne data
172 collection using high-resolution 3D airborne laser scanning is complementing spectral
173 information with structure[26]. Swarms of commercial cube satellites and the use of drones
174 to carry sensors are additional significant steps that complement these large-scale
175 programs (**Supplementary Note 1** "Earth Observation technology").

176 The increase in spatial resolution in the new sensors implies greater precision because
177 reference measurements taken within meter-scale plots on the ground can be matched
178 directly to meter-scale pixels[27]. This in turn improves the ability of EO to recognise
179 spatial gradients and boundaries.

180 Two additional factors affect the utility of remote sensing data for understanding
181 biodiversity change (**Supplementary Note 2** "Biodiversity and ecosystem information in
182 EO data"): affordability and access[22]. There has been a cultural shift, with free open
183 access on the rise. The opening of the Landsat archive in 2008 was a monumental
184 development[28], with ESA's Copernicus program following suit. Data access also refers to
185 the ability of users to retrieve, manipulate, and extract value from EO data. Cloud
186 computing and toolboxes are making these processes manageable, even with large data
187 archives.

188 The availability of copious EO data that have been shown in multiple studies to correlate
189 closely with on-the-ground measures of ecosystem structure, habitat condition, and even
190 animal communities (**Supplementary Note 2**) might suggest that remote sensors can be
191 used directly to define environmental indicators, but we must acknowledge that we are
192 still in the early stages of understanding how biodiversity delivers ecosystem functions
193 and services, and how they all respond to exogenous change. Directly observing
194 functional diversity is a partial solution but only with visible biodiversity such as
195 vegetation[26]. Thus, the challenge is to find ways to exploit the high efficiency and
196 information content of EO data while not falling prey to *reification fallacy* (**Box 2**), which
197 can arise when convenient but incomplete indicators are made available[29,30]. Our
198 institutions and reporting systems then retain the option to add and respond to new
199 knowledge.

200

201

202 ## Box 2. The Perils of Convenient Indicators

203 If we rely too directly on EO data, we run the risk of *reification fallacy*, in which a mere
204 indicator of a policy target itself ends up the target. Reification fallacy can reduce or
205 narrow conservation effort[31] and can crowd out future discoveries[32]. For example, while
206 remote sensing is an efficient and direct way to measure forest *cover* (Aichi Target 5:

reducing the loss rate of natural habitats), using forest cover and phenology to measure the contribution of biodiversity to carbon stocks (Target 15)[4] would ignore taxa invisible to satellites and could thus result in policymakers failing to exert the additional effort that is required to conserve saprotrophic fungal diversity, seed-dispersing mammals, and the seemingly inconsequential isopod, all of which have been implicated in boosting carbon storage[17,33,34]. More generally, land-cover class, which is a common EO-indicator, is a highly error-prone way to map and assess the complex processes supporting ecosystem services[35]. In short, convenient EO products could lead policymakers to focus only on that portion of biodiversity and ecosystem services that is directly observed by remote sensing, ignoring the rest.

High-Throughput Biodiversity Measurement

Most biodiversity, whether animal, fungal, plant, or microbial, and its many functions and services, is invisible to EO and will remain so for some time. But a growing number of efficient technologies are available for detecting and identifying biodiversity on the ground[36,37] (**Supplementary Note 3** "Biodiversity technology"). Automated bioacoustic and camera-trap recording devices (ARDs) can run continuously for weeks and accumulate thousands of records of invertebrates, birds, fish, reptiles, amphibians, and

mammals, and thus allow extended sampling of large areas at low workloads[38-42]. Alternatively, high-throughput DNA sequencers can be used in metabarcoding or metagenomic pipelines to detect and identify anywhere from one to thousands of species at a time from mass-collected, bulk samples of organisms (e.g. 'biodiversity soups'[43]), or from 'environmental DNA,' which is DNA liberated into the environment in the skin, hair, mucous, saliva, sperm, eggs, exudates, faeces, urine, blood, spores, root fragments, leaves, fruit, pollen, or rotting body parts of their original owners[44,45] (**Figure 2, Supplementary Note 3**). Multiple studies have now shown that metabarcode datasets reflect high-quality, morphologically identified biodiversity datasets sufficiently closely to allow correct management decisions, given best-practice protocols and controls[46-51].

The taxonomic identities, phylogenetic affinities, functional genes[52], spectral properties (of visible vegetation[26,53,54]), and/or co-occurrence patterns[55] of the detected species can be used to parameterise process-based production functions for ecosystem services[56-58] (**Figure 1**). For instance, the species identities and biomasses of wild bees identified metagenomically from bulk samples[59] could be combined with flower-use observation data[60] and detailed vegetation classification from EO to infer the availability and nature of local pollination services. Metagenomic data matched to identified species can be particularly powerful when the impacts of species loss on ecosystem function are not

243 random, evidence that has previously relied on intensive field sampling, e.g. in tropical
244 freshwater[61] and marine benthic communities[62].

245 Statistical Modelling as the Bridge

246 Earth Observation technology can produce large-scale, fine-resolution maps and dense
247 time series of a wide range of biophysical variables (**Supplementary Note 1 and 2**), but
248 it is difficult to translate the biophysical variables into biodiversity information. In
249 contrast, ARDs and DNA sequencing are capable of generating large amounts of
250 biodiversity information at species- or even individual-level resolution[63,64], but only from
251 point samples (**Supplementary Note 3**). Modern methods of statistical modelling allow
252 us to interpolate these point samples to build continuous species maps and to estimate
253 emergent metrics such as richness and dissimilarity[65-68], potentially also including
254 estimates of species abundance or biomass, depending on the sampling and analytical
255 methods used (**Supplementary Note 4** "Statistical modelling").

256 The three approaches with immediate potential are *Joint Species Distribution Models*[69-72]
257 (including *Latent Variable Models*), *Community Occupancy-Detection Models*[73], and
258 *Generalised Dissimilarity Models*[65,74] (**Figure 3**, **Supplementary Note 4**). Each approach
259 starts with a site-by-species matrix, from data that have been collected by ARDs or been
260 generated via metabarcoding or metagenomics (**Figure 2**, **Supplementary Note 3**), plus

any existing species distribution data. If some species are not detected, repeat sampling can be used to infer missing occurrences[73]. The site-by-species matrix is then paired with a corresponding site-by-environmental-covariate matrix, generated from continuous EO data plus any relevant geographical layers, and the two datasets are combined statistically to infer the joint distributions of multiple species across entire regions (**Figure 3**, **Supplementary Note 4**). All three approaches also provide a rigorous framework for quantifying sources of uncertainty and have already been applied successfully to conventionally acquired datasets (**Box 3**).

Box 3. Current Practice in Community Modelling

Ovaskainen et al.[71] used a joint species distribution model to predict the distributions of 55 butterfly species scored for presence/absence on a grid of 2609 10 X 10-km cells across Great Britain that had been sampled from 1995-1999 in a large citizen-science project. The model was successfully parameterised with a training dataset of just 300 cells and four environmental covariates (degree-days and three types of vegetation cover), plus spatially structured latent variables. Latent variables use observed species subgroupings to detect the effects of unmeasured environmental filters or species interactions such as competition. The parameterised model was used to predict butterfly

communities in the testing dataset, which consisted of the remaining 2309 grid cells. Together, the measured and latent variables explained an average of 42% of the variance in species occurrence (with medium-prevalence species more accurately predicted), and the two most dominant latent variables revealed a north-south gradient in species composition, with especially distinct communities in the southeast and northwest. Species richness per grid cell was accurately predicted, and the model's ability to discriminate presence and absence was high (mean AUC = 0.91).

Kéry and Royle[75] used community-occupancy modelling to analyse the 2001 Swiss breeding-bird survey while accounting for variation in detectability due to season, site, and species effects. The dataset consisted of 254 1-km^2 grid cells, each visited three times. The fitted model predicted each species' probability of occurrence as a function of site elevation and forest cover, as well as variance in the uncertainty of occurrence estimates, making it possible to estimate species distributions across the landscape and confidence in those estimates. Parameter estimates were naturally less precise for rare species, but information could be 'borrowed' from data-rich species to increase the precision of predictions for rare species. These procedures were able to compensate for the fact that only 134 total bird species had been detected in the survey, which is less than the true total of 163 species known to breed regularly in Switzerland, plus 22

298 occasional residents (the testing dataset). The occupancy-corrected model estimated that
299 between 1 and 11 species had been overlooked per grid cell and thus, that the true total
300 in 2001 was 169 species.

301 Mokany et al.[76] applied Generalised Dissimilarity Modelling (GDM) to a dataset of 2330
302 expert surveys of New Zealand land snails, which recorded 845 of 998 known species.
303 The GDM was parameterised with a training dataset of 2280 surveys and fourteen
304 environmental variables and explained 57% of the variation in beta diversity. In addition,
305 a generalised additive model parameterised on the training dataset explained 27% of the
306 variation in species richness (after scaling the 20 x 20-m survey quadrats to match the
307 area of modelling units (200 x 200-m); see discussion of scaling in **Supplementary Note**
308 **4**). Finally, the outputs were combined using a procedure called DynamicFOAM to assign
309 snail species to communities across New Zealand. Error was assessed by predicting
310 compositions in a testing dataset of 50 sites that had been held out of the model. On
311 average, the model was able to predict half the species that had been observed in each
312 cell, and the predicted total occupancy area per species was highly correlated with the
313 number of quadrat occurrences (Pearson's r = 0.902). When quadrats were pooled into
314 groups of 3 to 400 to reduce sampling stochasticity, predicted species richnesses almost
315 perfectly explained observed richnesses (R^2 = 0.99).

316

317

318 By mapping species distributions as the primary output, we do not lock ourselves into an
319 arbitrary set of convenient indicators, and ongoing discoveries on the relationship
320 between biodiversity and function, which are typically carried out at the species level, can
321 be added. As an illustration, the species diversity of wood-decaying fungi in natural
322 forests is notoriously difficult to assay but can be predicted in part by the volume and
323 species diversity of the stock of dead wood on the ground[77], and these environmental
324 covariates are partially quantifiable via airborne LiDAR sensors (**Supplementary Note**
325 **1**)[78], thus allowing EO-based inference of the distribution and level of wood-decaying
326 fungal diversity. Subsequent and unrelated research has suggested that pieces of dead
327 wood inhabited by a higher diversity of fungal species decompose more slowly, possibly
328 due to more intense interference competition[34]. Combining the two results suggests that
329 an EO-derived map of fungal species diversity could be used to contrast landscape
330 management options for how well they conserve saprotrophic fungal biodiversity and
331 thus enhance carbon storage.

332 Two further reasons for focusing on species-resolution maps as the primary output are
333 that the regional species pool (*gamma diversity*) and the biological dissimilarity of sites

(*beta diversity*) could contribute to maintaining functional stability[58,79,80] and that species-resolution outputs retain the option of aggregation to represent different aspects of biodiversity, including higher-taxonomic, functional, and phylogenetic groupings[81].

Many methods are also available to predict *individual* species ranges, and EO can help improve their accuracy, as shown by an example[82] combining MODIS satellite data with environmental DNA to map an invasive diatom over a watershed [Target 9, invasive species pathway identified] (**Supplementary Figure 3.1**). However, ecosystem functions and services are rarely delivered by only one species, and simply summing the outputs of individual models to simulate communities is computationally inefficient, statistically flawed, and does not account for species interactions[83].

From CEOBE to Aichi

In essence, our argument is that new technologies make the new community-modelling approaches (**Box 3, Figure 3**) widely feasible, especially in biodiversity hotspots, where it is particularly difficult to generate large datasets. Larger numbers of environmental covariates and species together increase explanatory power by providing a greater breadth of predictors, and by exploiting latent variables and letting rare species 'borrow' information[42,75,84], respectively. As a result, continuous streams of EO data can be more powerfully interpreted to track biodiversity status and trends (**Figure 1**).

352 The predictive performance of fitted models can be cross-validated by rounds of
353 comparison with testing datasets that were either split from the model-training
354 dataset[71,76] or derived from historical and expert knowledge[75], and thus, the adequacy of
355 the input data and sampling design, or conversely the degree of model uncertainty, can
356 be assessed *post hoc* (**Box 3**). The regularly updated biodiversity maps that are the
357 primary outputs of the CEOBE approach (**Figure 1**), plus the quantified uncertainty in
358 those maps, can then be incorporated into a larger process of structured decision
359 making and adaptive management[85-87] to (1) identify likely consequences of proposed
360 actions by observing natural experiments that mimic those actions, (2) compare observed
361 results of management interventions against objectives, and (3) help identify and tackle
362 sources of uncertainty.

363 An early example of the CEOBE approach is given by Sollmann et al.[42], who used
364 community-occupancy modelling to connect environmental covariates from the 5-m-
365 resolution RapidEye satellite to point-sample data from camera traps in three tropical-
366 forest logging concessions in Sabah, Malaysian Borneo, one of which has been managed
367 to reduced-impact-logging standards set by the Forest Stewardship Council (Aichi Target
368 7, sustainable management under forestry). The dataset consisted of detection events for
369 28 mammal species at 166 camera-trap stations, each station scored using EO data for

distance to water, distance to oil-palm plantation, and forest condition. Estimated relationships between species occurrence and the three covariates were used to predict species occurrence across the three reserves, with rare mammal species borrowing information from more common ones. Species richness was estimated to be higher in the FSC-certified reserve, particularly for threatened species (Target 12, improved conservation status of threatened species). The percentage of area occupied, which could indicate larger population sizes, was also estimated to be higher in the FSC-certified reserve for the majority of species, including for some highly endangered species like the Sunda pangolin *Manis javanica*. Finally, the modelled species richness maps were found to correlate strongly with EO-estimated aboveground biomass at the large spatial grain of whole reserves, but not at a finer resolution (potentially due to hunting at reserve borders), further demonstrating the critical contribution of ground-level point samples for linking pure-EO data to biodiversity.

The major remaining components of uncertainty relate to generalisability, because only a single FSC-certified reserve was sampled; the applicability of results to arboreal species, which tend to be detected more frequently in forests with disturbed canopy but are not necessarily more widespread in these forests; and wide confidence intervals around parameter estimates for some species as a consequence of sparse data and a fairly

388 complex hierarchical model. This example serves as a proof of concept that camera
389 trapping and occupancy modelling can be used to assess biodiversity conservation based
390 on species maps, and the approach has been incorporated in the ten-year forest
391 management plan and wildlife monitoring strategy for the FSC-certified area. Repeated
392 surveys will help to narrow uncertainties in the model, and a future power analysis is
393 planned to estimate the sampling effort required to detect trends and/or provide
394 estimates with a desired level of certainty[88].

395 Another example of the CEOBE approach is the use of Generalised Dissimilarity
396 Modelling to connect EO-derived metrics of habitat degradation and fragmentation[89,90]
397 to over 300 million records of more than 400,000 species from the Global Biodiversity
398 Information Facility (www.gbif.org) and the Map of Life (mol.org)[91]. The GDM models
399 spatial turnover in biodiversity composition at 1-km-resolution globally, and by invoking
400 the assumption that terrestrial biodiversity declines according to the classical species-
401 area power function, the GDM estimates the proportion of biodiversity that has been
402 retained in each grid cell after habitat loss, based on the proportion of similar habitat
403 remaining unimpacted within the landscape[92]. This metric thus tracks whether rates of
404 loss, degradation, and fragmentation of natural habitats are being reduced (Aichi Target
405 5). Further, by combining this approach with a global database of protected-area

406 coverage (www.protectedplanet.net), it is possible to report progress against Target 11,
407 which aims for protected areas to cover areas of particular importance to biodiversity
408 and ecosystem services and to be ecologically representative and connected (see also
409 Ref. 93). An important caveat is that the biodiversity data in this case are historical in
410 nature and thus contain the taxonomic and sampling biases and constraints of the past
411 (**Box 2**). Ideally, the biodiversity data will transition to up-to-date, properly sampled, and
412 more taxonomically comprehensive point samples.

413 Of course, CEOBE outputs cannot contribute to all Aichi Targets, namely those that are
414 focused on policy, planning, and funding reform (Targets 2, 3, 4, 20), the conservation of
415 genetic cultivars (Target 13), the alleviation of climate-change pressures on coral reefs
416 (Target 10), benefits sharing (Target 16), and the integration of traditional knowledge
417 (Target 18). It also remains to be seen how well or poorly EO data reflect biodiversity in
418 aquatic ecosystems (Targets 6 and 11), although environmental DNA on its own is a
419 highly promising source of data on aquatic biodiversity. On the other hand, the efficient
420 production of biodiversity maps and open access to analytical pipelines will help to
421 disseminate the science base and technologies related to biodiversity (Target 19), and
422 could contribute to public awareness of efforts to conserve biodiversity (Target 1) and
423 improve the efficiency of national biodiversity planning (Target 17).

Conclusions

It is extremely difficult to identify all the species present in a location (*the Linnaean challenge*), to delimit the geographic distributions of species (*the Wallacean challenge*), and to quantify their responses to natural and anthropogenic environmental change (*the Hutchinsonian challenge*)[94]. A synergy of Earth Observation, automated recording devices, high-throughput DNA sequencing, and modern statistical modelling can meet these challenges by making it possible to scale up from data-rich but finite sets of point samples to spatially continuous biodiversity maps, which are more informative than a few convenient indicator species but still let us generate summary statistics to communicate trends to decision-makers and the general public. The use of formal statistical frameworks lets us quantify error, identify gaps in our understanding, objectively rank the most likely pressures on biodiversity from multiple candidates, and increase the robustness of change detection. Adding information on species interactions and functions helps link biodiversity to ecosystem functions and services (**Box 1, Figure 1**) in a process-based approach[56], rather than relying on crude estimates from land classes[35]. Finally, as DNA-based technologies mature, the same samples could track population-genetic diversity[64,95,96].

441 A global, multi-resolution monitoring network is thus within our reach but will still
442 involve a number of challenges associated with technical capacity, computation and data
443 storage, and data standardisation. For every ecologically distinct region, there will be an
444 initial cost to collect data for model parameterisation, followed by a low level of
445 continuous sampling, which will be necessary for updating models and for surveillance
446 monitoring of environmental drivers that are invisible to EO, such as broad-spectrum
447 insecticides. The initial costs are probably best borne by governments, as part of their
448 commitment to the Convention on Biological Diversity, and there is great promise in
449 using citizen-science networks to collect standardised, bulk biodiversity samples over
450 large areas. A laudable example is the School Malaise Trap Program that recruited
451 hundreds of secondary-school science classes to collect arthropods across Canada
452 (malaiseprogram.com). Initial investment could also come from existing monitoring
453 budgets with the expectation that additional information content will compensate for
454 reduced sample numbers within existing programs[82]. The follow-up continuous sampling
455 requires steady funding streams, and the standardisation of the CEOBE approach meets
456 the needs of international certification schemes, such as REDD+, Climate, Community &
457 Biodiversity Standards, Forest Stewardship Council, and the Roundtable on Sustainable
458 Palm Oil, which all require the continuous monitoring of biodiversity and ecosystem

459 services. Biodiversity-offset payments to mitigate the impacts of development and
460 carbon emissions are also expected to provide funding streams, and standardised
461 assessments are needed to ensure that offsetting results in biodiversity net gain[97].

462 The CEOBE approach also depends on institutional support for the multidisciplinary
463 collaborations needed to generate, combine, analyse, and act upon data from disparate
464 disciplines (EO, ARDs, genomics, taxonomy and systematics, ecosystem functions and
465 services, statistics, and decision science), expertise that no single individual has[12,30,98].
466 Identifying causal determinants of species distributions needs a clear understanding of
467 phylogenetic structure and functional diversity, the ecological processes involved, and
468 what EO sensors can and cannot observe[99]. Expert knowledge will also contribute to
469 sampling design and covariate selection so that the full breadth of environmental
470 conditions is captured, especially those not visible to EO.

471 On the other hand, collaborations need not be global. Political and social interests will
472 vary by region, and agencies should be encouraged to trial CEOBE within their
473 jurisdictions where there are clear opportunities to improve management, while also
474 enforcing the publication of primary data and analytical pipelines[27,100]. The
475 Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) could play an
476 important role as a global coordinating institution.

Resources for environmental management are always likely to be limited, but by doing more with our expensively gained field data, we can take action more efficiently and effectively. What is required now is leadership by governments and international organisations to stimulate integrated research and to endorse the use of comprehensive biodiversity information[6].

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Author Contributions

BC and HB led the sections on Earth Observation technology. KB and DWY led the sections on Biodiversity technology. AB led the sections on Statistical modelling. AB, RS, AW, OO, and DWY led the sections on case studies (Box 3 and CEOBE to Aichi). CM led the Conclusions section. Figures were created by KB, AB, CC, and AZ. All authors contributed to multiple rewrites, with a large contribution by DR. AB and DWY wrote the first draft and supervised the work.

Additional Information

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Competing Interests

DWY and AV are co-founders of a private company that provides commercial metabarcoding services.

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797

Figure legends

Figure 1. CEOBE – Connecting Earth Observation to Biodiversity and Ecosystems. Top row left: EO data and other geographical datasets are used to generate spatially continuous maps of biophysical data (**S1, S2**). **Middle row left**: A real landscape with point-sample locations indicated by yellow dots. **Bottom row left**: Biodiversity is recorded manually using traditional methods, automated audio or image recording devices, or metabarcoding or metagenomic pipelines to generate a site X species table (**Figure 2**, **S3**). However, most of the landscape is not sampled (empty rows in the table). **Right side**: The point samples are combined statistically with continuous biophysical maps to predict biodiversity composition over the whole landscape (**S4**). In combination with ancillary data like trait databases, process-based models can then identify the functional composition of any location and map the expected distributions of ecosystem functions and services.

Figure 2. Metabarcoding and metagenomic processing pipelines for high-throughput biodiversity surveys. Top row: Point locations across a landscape are sampled for biodiversity, and DNA is separately extracted from each sample. Three common sample types are (i) bulk samples of arthropods (depicted here), (ii) environmental DNA (eDNA)

from soil, water, and air, and (iii) invertebrate collectors of vertebrate DNA (iDNA), such as mosquitoes, leeches, flies, dung beetles, and ticks. **Left column**: Metabarcoding – Each sample's DNA is amplified via PCR (polymerase chain reaction) for a particular marker gene that is taxonomically informative, the samples are pooled and sequenced on a high-throughput sequencer, and then sorted back to sample by the sample-specific tags added during PCR. The sequences are then clustered into Operational Taxonomic Units (OTUs), which are species hypotheses, and assigned taxonomies by matching against online databases. **Right column**: Meta/mitogenomics – Each sample's total DNA is sequenced, and the output DNA reads are matched to reference genomes, which are often mitochondrial genomes. **Bottom row**: The output of both processing pipelines is a 'sample X species' table. Metabarcoding pipelines are useful for general biodiversity discovery and surveys because online barcode databases are more taxonomically complete, and even without taxonomic assignment, it is possible to calculate community metrics from OTUs only. Metagenomic pipelines are more costly, but advantageous when it is important to reliably identify particular sets of species and to a greater extent preserve relative biomass information. See **S3** for further details. Clip-art courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

833 **Figure 3. Three statistical pathways to map community composition and summary**

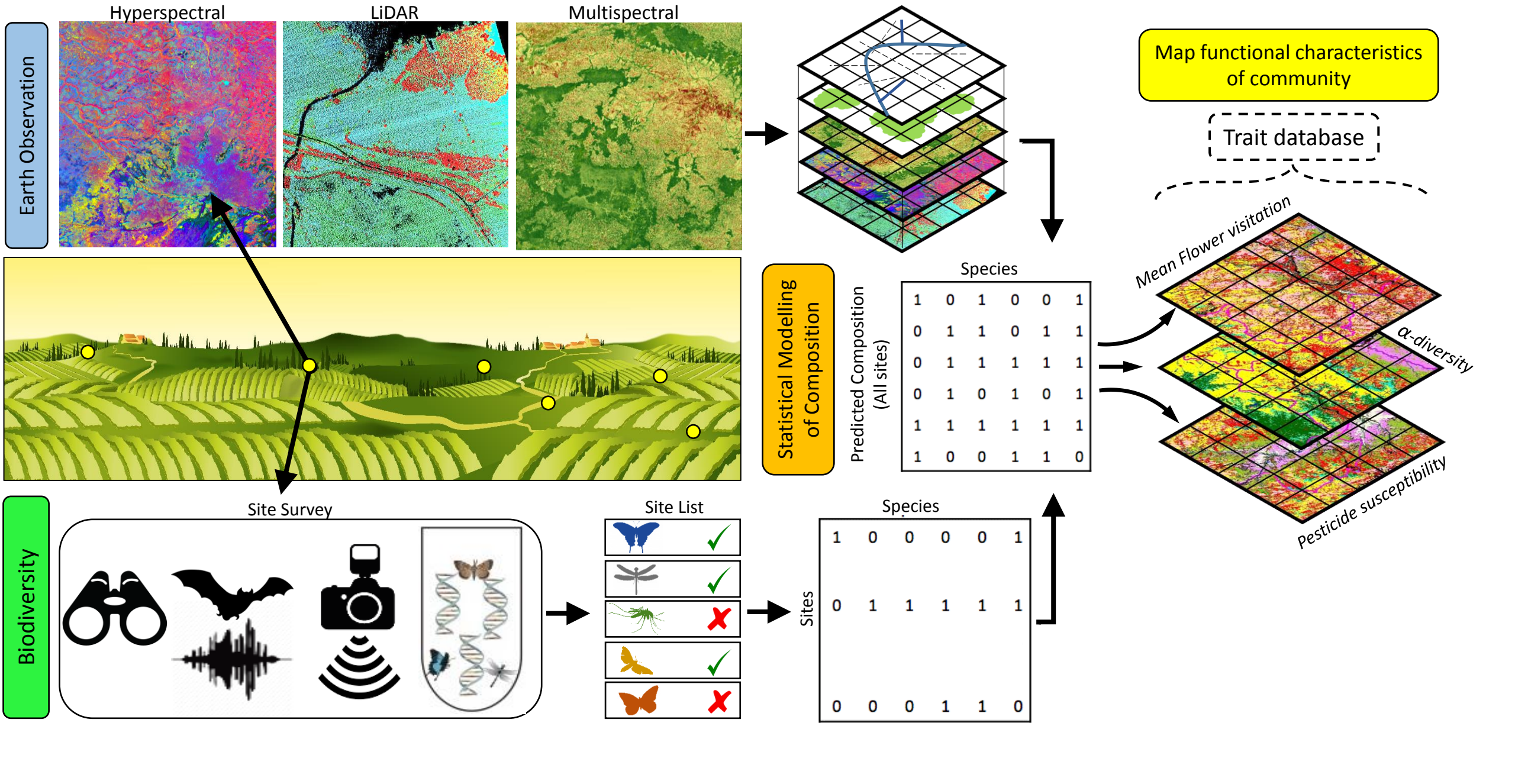
834 **metrics from the combination of biodiversity point samples and continuous Earth**

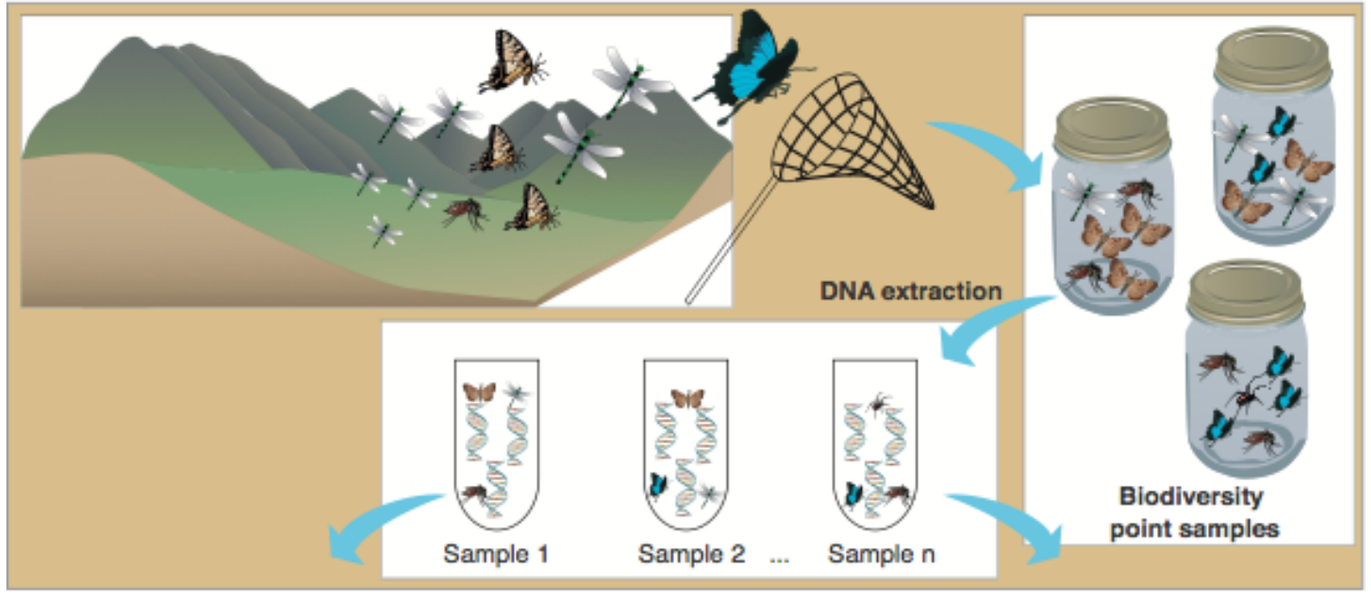
835 **Observation (EO) maps**. Local diversity – α; species turnover – β; and regional diversity –

836 γ. For clarity, the figure only considers models for species occurrence (OCC), not

837 abundance. GAM: Generalised Additive Model. DynamicFOAM is described in Ref. 76.

838 See **S4** for further details.

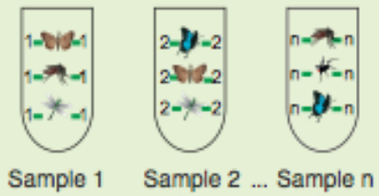

Earth Observation
Hyperspectral
LiDAR
Multispectral
Map functional characteristics of community
Trait database
Mean Flower visitation
α-diversity
Pesticide susceptibility
Statistical Modelling of Composition
Predicted Composition (All sites)
Species
1 0 1 0 0 1
0 1 1 0 1 1
0 1 1 1 1 1
0 1 0 1 0 1
1 1 1 1 1 1
1 0 0 1 1 0
Biodiversity
Site Survey
Site List
Species
Sites
1 0 0 0 0 1
0 1 1 1 1 1
0 0 0 1 1 0

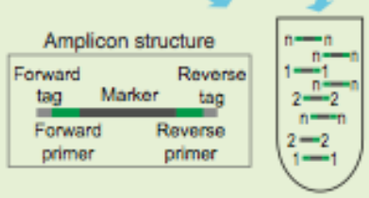


Metabarcoding

Only sequence specific gene regions (markers)
for specific taxonomic groups (e.g the Insecta)

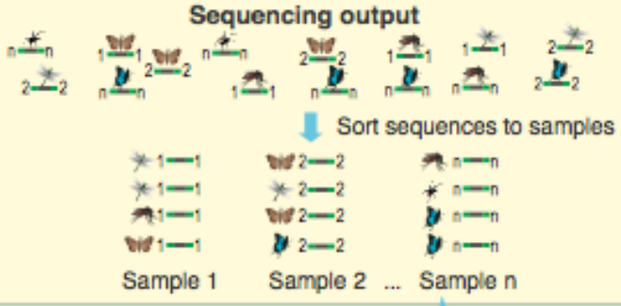
PCR with tagged primers for taxonomic target group





Sequencing

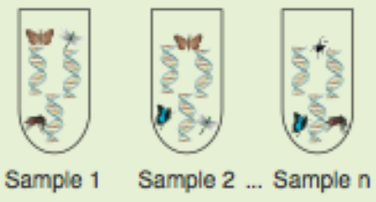
Sequencing output



Meta-/mitogenomics

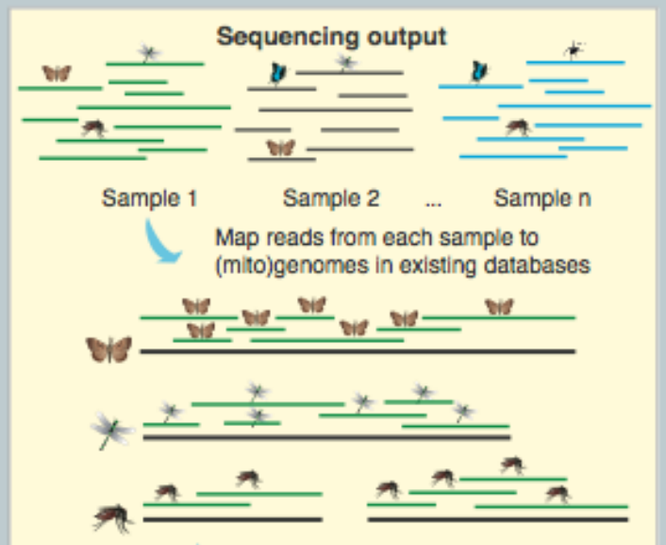
Sequence total DNA

Total DNA



Sequencing

Sequencing output



Metabarcoding is a targeted and cost-effective approach in which only short marker(s) for the taxonomic groups desired for a given biodiversity assessment are sequenced. It is more likely to detect low-biomass taxa than is mito-/metagenoimics. Metabarcoding exploits existing reference databases, which are larger than reference database collections for whole (mito)genomes.

Species

Sample											
	0	1	0	1	0	0	1	0	1	1	0
	1	0	0	0	0	1	0	0	0	0	0
	1	0	1	0	1	1	1	1	0	1	1
	0	1	0	0	0	0	0	0	1	0	0
	1	1	0	1	1	1	1	1	1	0	1
	0	0	0	1	0	1	0	1	1	0	0
	1	0	0	0	0	1	1	0	0	0	0

Meta-/mitogenomics requires deeper sequencing than metabarcoding because total DNA is sequenced, and only a small fraction of the sequencing output is used for detecting species.
Meta-/mitogenomics relies on whole (mito-)genome reference databases, but when these are available, it has higher certainty of taxonomic assignment than does metabarcoding.

Joint Species Distribution Models / Latent Variable Models

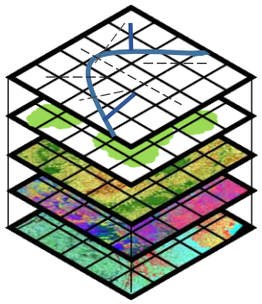
Biodiversity point samples

Species

Sites

1	0	0	0	0	1
0	1	1	1	1	1
0	1	0	0	0	1
0	0	0	1	1	0

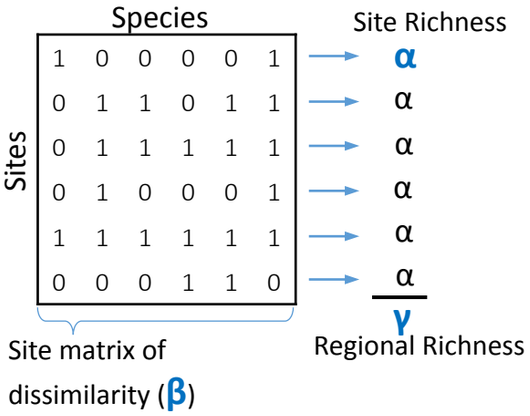
EO Spatial covariates



$$OCC = f(Site\ covariates) + f(Latent\ Variables)$$

Species distributions are described as a function of unobserved latent factors as well as observed covariates. Account for species covariance, but do not easily account for differences in species detection.

Predicted probabilities of species occurrences at all sites



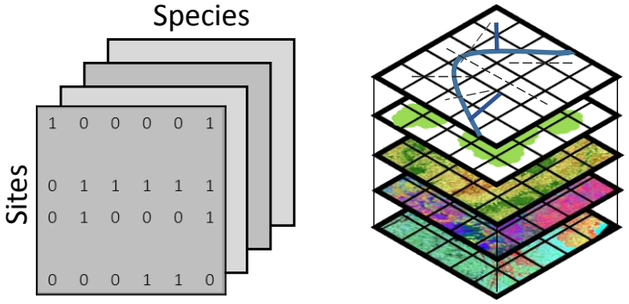
Occupancy-Detection Models

Biodiversity point samples with repeated surveys

Species

Sites

EO Spatial covariates



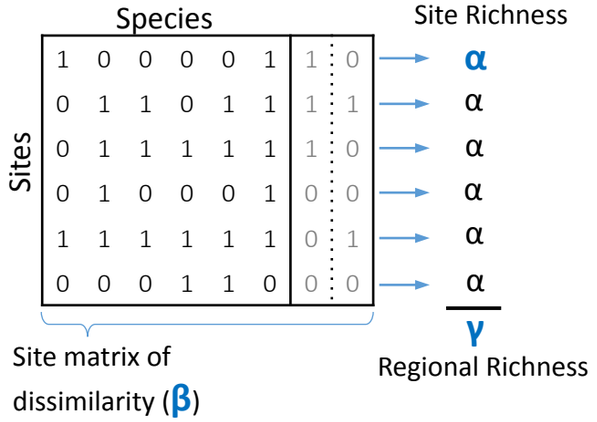
Site covariates

Survey covariates

$$OCC = Occupancy.model * Detection.model$$

Environmental covariates can describe both a species' distribution and how that distribution is observed, which itself can depend upon survey characteristics. Account for imperfect detection, but treat species independently.

Predicted probability of species occurrence at all sites (including unobserved species)



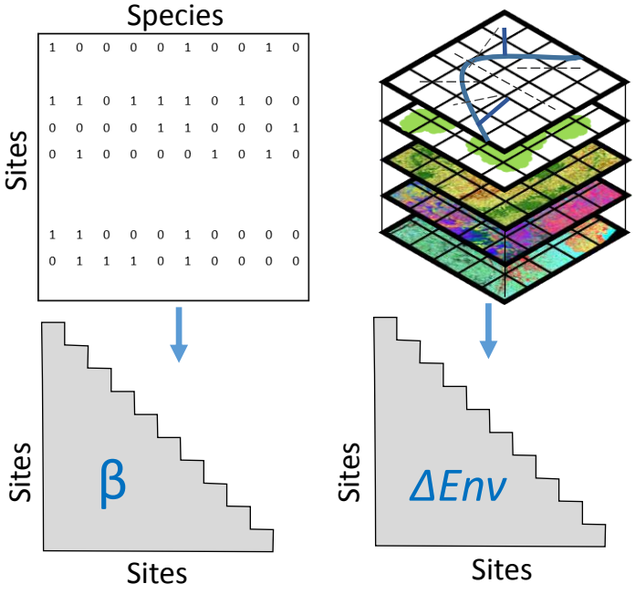
Generalised Dissimilarity Models

Biodiversity point samples (high species diversity)

Species

Sites

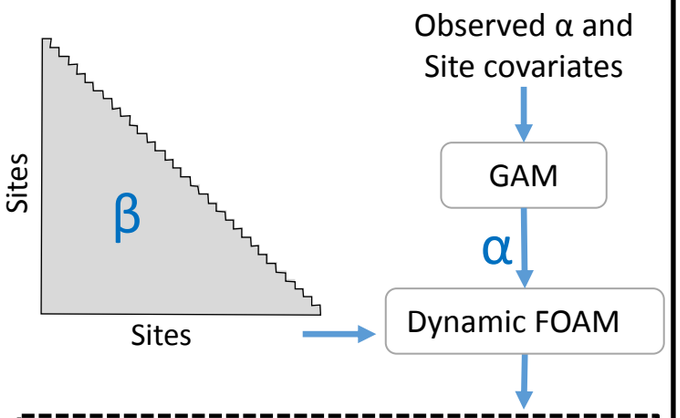
EO Spatial covariates



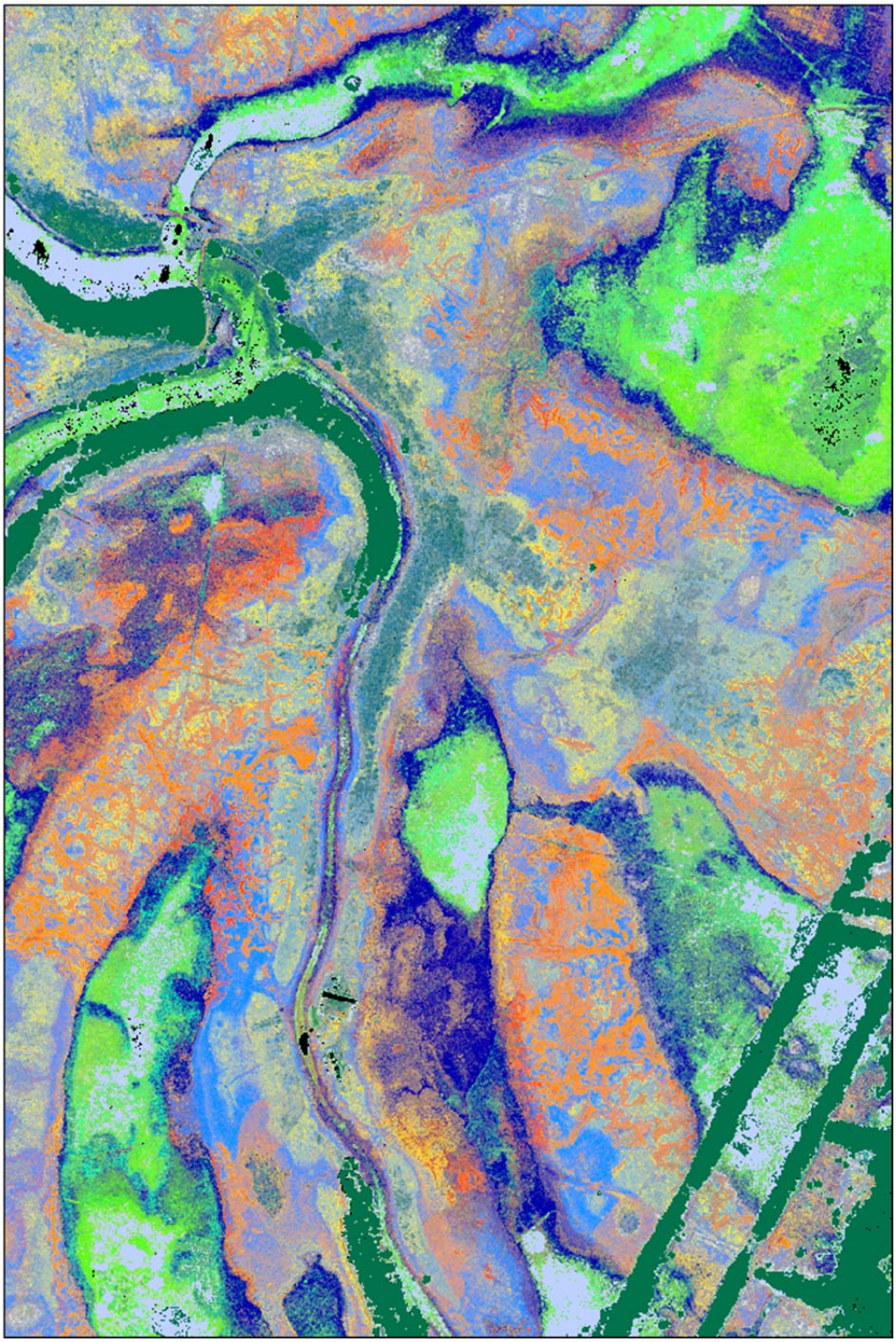
$$\beta_{ij} = f(\,|Envi - Envj|)$$

Compositional dissimilarity (β) between each pair of sites (*i* and *j*) is a function of the difference in environmental conditions (*ΔEnv*).

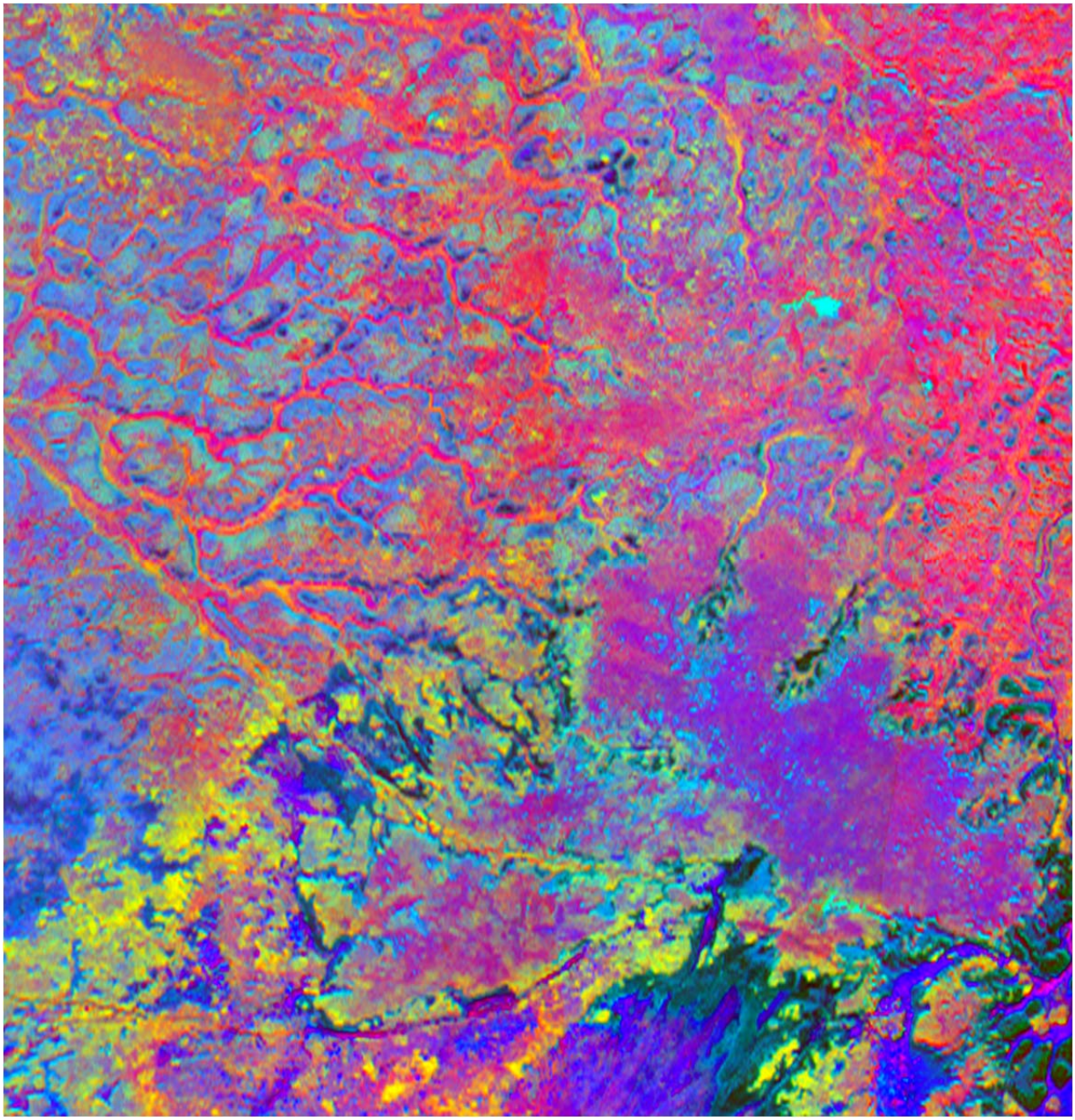
Predicted compositional dissimilarity between any pair of sites (β)



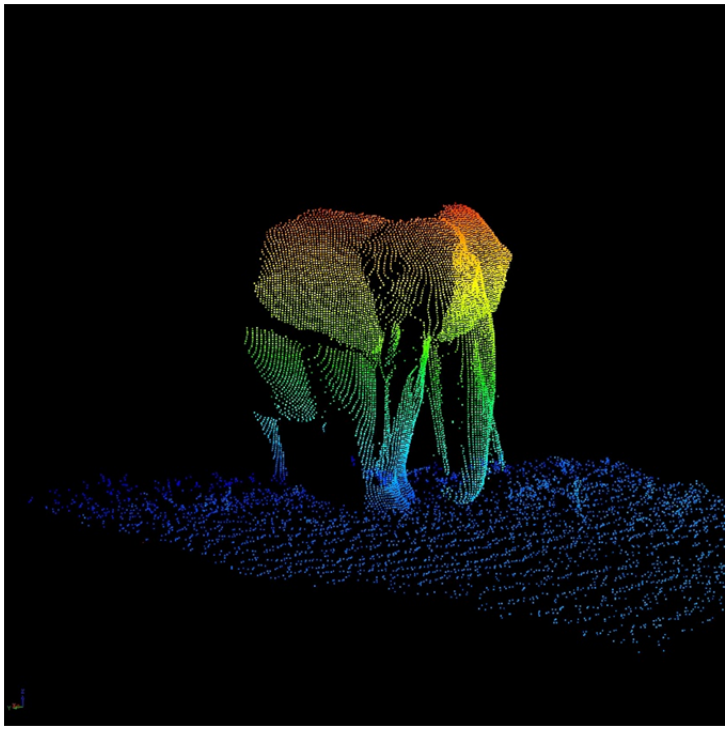
Predicted composition of all sites consistent with patterns of α and β

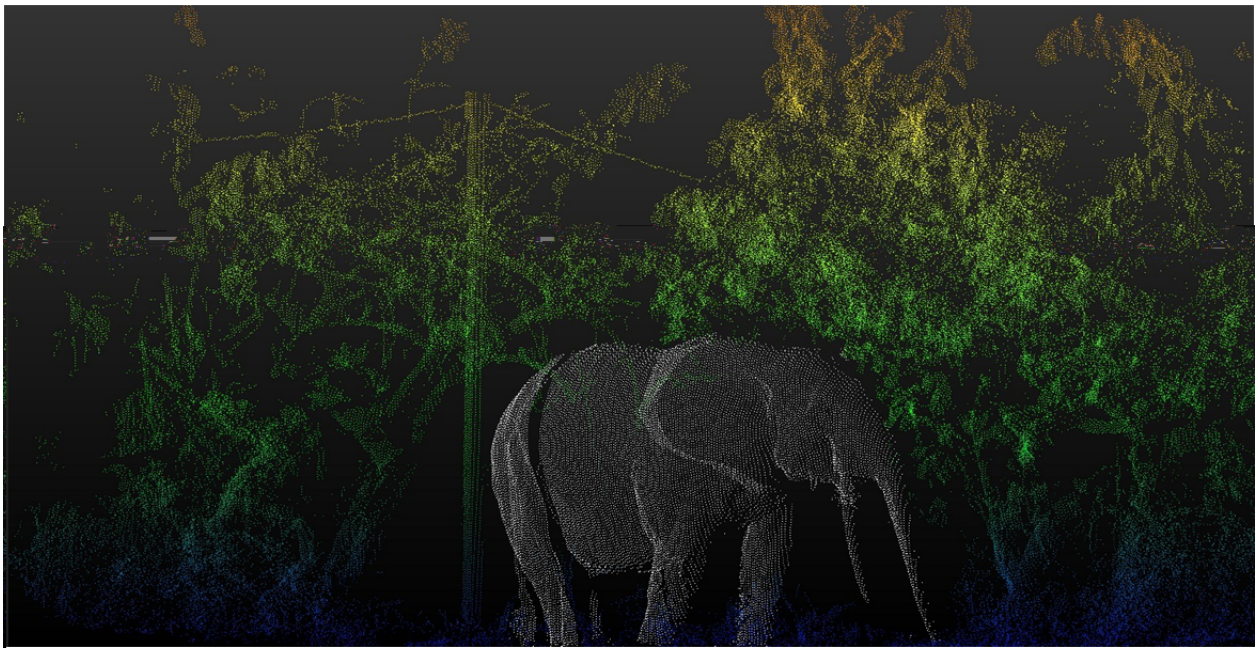


Fuzzy classification of grassland vegetation in an alkaline grassland in Püspökladány, Hungary, based on airborne LIDAR. Colours represent the weighted probability for a given vegetation class in each cell (0.5m2) (photo credit: András Zlinszky).



Vegetation composition of a peatland using Partial Least Square Regression models on a hyperspectral image. The image is a false colour composite showing the predicted abundance of Graminoids (Red), Shrubs (Green), and Bryophytes (Blue) (photo credit: Beth Cole).





A forest elephant “scanned” during a terrestrial laser-based measurement of a tropical rainforest in Gabon 2013 (photo credit: Kim Calders).